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David S. Moore

*Pitzer College*

Chris Moore

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grounding mechanism, as predicted by empiricist accounts only.

In conclusion, although pre-existing circuits might be reused to provide representational resources for novel functions, we propose that these resources remain insufficient, and possibly unspecified, without the involvement of sensorimotor experience. In order to obtain a more universal theory of neural reuse, future studies now have to clarify how representational resources are shaped by cultural and educational constraints and how they interact with the functions they support.

## Neural reuse as a source of developmental homology

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David S. Moore<sup>a</sup> and Chris Moore<sup>b</sup>

<sup>a</sup>Department of Psychology, Pitzer College and Claremont Graduate University, Claremont, CA 91711; <sup>b</sup>Department of Psychology, Dalhousie University, Halifax, NS B3H4J1, Canada.

dmoore@pitzer.edu Chris.Moore@Dal.Ca

http://pzacad.pitzer.edu/~dmoore/

http://myweb.dal.ca/moorec/index.html

**Abstract:** Neural reuse theories should interest developmental psychologists because these theories can potentially illuminate the developmental relations among psychological characteristics observed across the lifespan. Characteristics that develop by exploiting pre-existing neural circuits can be thought of as developmental homologues. And, understood in this way, the homology concept that has proven valuable for evolutionary biologists can be used productively to study psychological/behavioral development.

Conventional wisdom in the neurosciences has long held that specific brain regions have specific functions. However, several recent studies have undermined the claim that cognitive functions can typically be mapped in straightforward ways to highly specialized brain areas, leading Anderson (2007c) to propose his massive redeployment hypothesis (MRH). In the target article, Anderson has considered his theory, along with others that posit similarly, that existing neural structures are normally reused/recycled/redeployed as new brain functions develop. This new approach has enormous potential for helping neuroscientists rethink the relationship between brain structures and their functions, as well as for helping those interested in the development and/or evolution of behavioral organization to understand changes in that organization across ontogeny and phylogeny.

Anderson uses the MRH to predict that a brain area's phylogenetic age should correlate with how often that area is deployed for various cognitive functions, and that a cognitive function's phylogenetic age should correlate with how localized that function is in the brain. However, although Anderson recognizes that neural reuse theories bear on questions of development, his article focuses on phylogeny to the virtual exclusion of ontogeny. Brief mentions of development are made, and a note points out that neural reuse "is broadly compatible with the developmental theories of Piaget" (target article, Note 10); but, in fact, neural reuse should interest all developmental psychologists because the approach is compatible with most current theories of development and could contribute to theoretical progress in the field in general. Anderson cites Dehaene's "neuronal recycling" theory as having potentially identified a "fundamental developmental . . . strategy for realizing cognitive functions" (sect. 1, para. 3); but, like other promissory notes in Anderson's text, this one is never fully redeemed. Neither Anderson nor Dehaene and Cohen (2007) fully consider the implications of neural reuse theories for understanding development.

The idea of neural reuse could have profound and general implications for the understanding of behavioral development.

In particular, we believe that neural reuse produces a type of developmental homology, and that just as evolutionary biology has profited from the discovery and analysis of evolutionary homologies (Hall 2003), so developmental psychology may profit from the identification of developmental homologies, some of which likely arise as a result of neural reuse. Because two or more psychological characteristics present at a given point in development might both (re)use neural circuits formed much earlier in development, thinking about such characteristics in terms of developmental homology could well illuminate their relationship to each other (as well as to other psychological characteristics present earlier in development that also depend on these circuits). Consequently, we believe that importing the concept of homology into developmental psychology has the potential to help behavioral scientists understand when, how, and why specific traits have common developmental origins.

Within biology, several types of homology have been identified, including among others (1) taxic homology (Griffiths 2007), in which characteristics in different species (e.g., bat wings and human forearms) have derived from a characteristic present in a common ancestor; (2) serial homology (Rutishauser & Moline 2005), in which parts of an individual organism are of the same type (e.g., the corresponding bones in a person's right hand and right foot, or any two vertebrae in mammalian spinal columns); and (3) ontogenetic homology (Höbfield & Olsson 2005), in which distinct individuals of the same species have differing features that nonetheless derive from common embryonic tissues (e.g., human ovaries and testes). Developmental homologies arising from neural reuse would be most similar to the kinds of homologies identified by Bertalanffy in 1934 (described in Höbfield & Olsson 2005), and would include pairs of psychological characteristics, both of which emerged from a common characteristic present earlier in development. In addition, much as human forearms are homologous to the forearms of extinct Australopithecines, psychological characteristics of adults could be recognized as homologues of psychological characteristics present in juveniles in various developmental stages. Such homologues *could* arise in ways that would not require neural reuse – after all, "a structure that is homologous across species can develop based on non-homologous genes and/or developmental processes, and vice-versa" (Brigandt & Griffiths 2007, p. 634) – but any characteristics known to emerge following the redeployment of a specific neural circuit would seem *prima facie* to be homologous, at least structurally if not functionally.

Several examples of possible developmental homologies may be identified. Temporal cognition in the form of episodic thinking develops later than spatial cognition and makes use of related conceptual structures (Clayton & Russell 2009). The discovery that these mental processes also make use of certain shared neural circuits would indicate that they are homologous, thereby shedding light on the nature of their developmental relationship. Linguistic structures, likewise, may well depend upon earlier-developing social interactive communicative structures. Tomasello (2003), for example, argues that syntax can be understood as a form of joint attention, a conceptualization that implies that these are homologous psychological characteristics, their different appearances notwithstanding. Still other psychological characteristics that appear similar across age have been assumed to be homologues, such as the neonatal imitation reported by Meltzoff and Moore (1977) and later-developing forms of imitation observed in older children and adults. Even so, studies of the neural circuits that contribute to neonatal and later imitation might or might not support this conclusion; a finding that adult imitation normally recruits neural circuits previously used during neonatal imitation would certainly qualify as support for the contention that these behaviors are homologous.

As Anderson suggests, neural reuse might be a fundamental organizational principle of the brain; and just as this idea can be used to formulate testable hypotheses about the evolution of

both the brain and its function, we think it could also influence the study of psychological development in significant ways. Similarly, importing the idea of homology from evolutionary biology into developmental psychology could help researchers conceptualize behavioral development in new and potentially informative ways. Taken together, the concepts of neural reuse and developmental homology could be used to further our understanding of brain development, psychological development, and the relationships between these phenomena.

## Reuse of identified neurons in multiple neural circuits

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Jeremy E. Niven<sup>a</sup> and Lars Chittka<sup>b</sup>

<sup>a</sup>Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, United Kingdom; <sup>b</sup>Research Centre for Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, United Kingdom.

jen22@cam.ac.uk l.chittka@qmul.ac.uk

<http://www.neuroscience.cam.ac.uk/directory/profile.php?jen22>

<http://chittkalab.sbcs.qmul.ac.uk/>

**Abstract:** The growing recognition by cognitive neuroscientists that areas of vertebrate brains may be reused for multiple purposes either functionally during development or during evolution echoes a similar realization made by neuroscientists working on invertebrates. Because of these animals' relatively more accessible nervous systems, neuronal reuse can be examined at the level of individual identified neurons and fully characterized neural circuits.

The principle of neural reuse is widespread within peripheral sensory and motor circuits in both vertebrates and invertebrates. Peripheral sensory circuits, such as those in the retina, extract and process information that is used in many behaviors. Indeed, the coding of visual scenes or odors requires that overlapping sets of sensory neurons are activated in response to different scenes or odors. Likewise, overlapping sets of premotor and motor neurons may be activated in disparate behaviors that require activation of overlapping sets of muscles.

The detailed characterization of invertebrate neurons and neural circuits has demonstrated that neurons can be reused to form neural circuits that perform multiple functions. One striking example comes from the stomatogastric ganglion (STG) of the crab *Cancer borealis*. The ~30 neurons of the STG control rhythmic muscle activity involved in chewing and digestion of food – the gastric mill and pyloric rhythms, respectively. Individual identified neurons may contribute to the production of more than one rhythm. The VD neuron, for example, is involved in the generation of both the gastric mill and pyloric rhythms (Weimann & Marder 1994). Thus, the dynamic restructuring of neural circuits within the STG provides a clear example of the reuse of neurons for the production of different behaviors.

Reuse may also be found in neurons involved in learning and memory. In the pond snail (*Lymnaea stagnalis*), the breathing rhythm is generated by three synaptically connected neurons that form a central pattern generator. One of these neurons, RPeD1, is also necessary for many aspects of learning and memory; and removing the RPeD1 cell body can prevent the formation or reconsolidation of long-term memories (Sangha et al. 2003). In honeybees (*Apis mellifera*), a single identified neuron (VUMmx1) in the suboesophageal ganglion mediates the reward pathway in associative olfactory learning, but this neuron has also been implicated in learning phenomena as diverse as second-order conditioning and blocking (Menzel 2009).

The above examples emphasize that within the adult nervous system neurons are reused for different functions; but as Anderson points out, neurons may also be reused during development.

One such example is the reuse of larval motor neurons in the adult nervous system of the tobacco hornworm moth (*Manduca sexta*). *Manduca* caterpillars, like those of all moths and butterflies, undergo a metamorphosis that involves restructuring of the nervous system. Motor neurons that innervate leg muscles in the caterpillar have been shown to remodel their axons and dendrites during metamorphosis before innervating newly developed leg muscles (Kent & Levine 1993). Memories can also be retained between larval and adult forms of insects, despite the remodeling of neural networks during metamorphosis. For example, adult fruit flies (*Drosophila melanogaster*) retain memories of odors associated with aversive stimuli formed as third instar larvae (Tully et al. 1994). Memory retention between developmental stages suggests that those elements of neural circuits that are the loci of these stored memories are reused in adult animals.

Anderson also suggests that neurons may be reused during evolution, acquiring novel functions and possibly losing their original function. Again, invertebrate neural networks provide examples of such reuse during evolution. In the desert locust (*Schistocerca gregaria*), more than 20 interneurons have been identified from the neural networks controlling the flight muscles. Some of these interneurons have homologues in abdominal neuromeres, which innervate segments that do not bear wings or contain motor neurons innervating flight muscles (Robertson et al. 1982). Yet, these interneurons can reset the flight rhythm in the locust, showing that despite their location they are components of the flight control machinery. Indeed, their role in the flight control circuitry may have influenced the structure of the insect ventral nerve cord (Niven et al. 2006). Robertson et al. (1982) have suggested that these interneurons are remnants of control circuits for ancestral appendages that have been lost.

Neural reuse may be more prevalent in invertebrate brains, especially those of insects, which contain relatively few neurons compared to those of many mammals. Many insects possess small brains that have been miniaturized during evolution (Beuthe et al. 2005). Their small size means that insects are under selective pressure to reduce energetic costs and brain size (Chittka & Niven 2009). Anderson suggests that energy minimization in the absence of behavioral constraints would promote the reduction of neural structures and, thereby, the reuse of neural substrates. The possibility of reusing neurons for different behaviors through the dynamic restructuring of neural circuits means that the consequences of miniaturization may not be as severe as is often assumed.

Anatomical modularity is clear within invertebrate nervous systems (e.g., Niven et al. 2006) but, as Anderson mentions, neural reuse may blur the boundaries between anatomical modules. Indeed, most behaviors involve sensory and motor circuits that are overlapping anatomically, and it seems unlikely that the majority of behaviors are localized entirely within specific anatomical modules. As discussed above, the locust neurons involved in wing control, which include examples of evolutionary reuse, are spread across six neuromeres although only two segments bear wings (Robertson et al. 1982). Indeed, even reflex arcs confined to a single neuromere can be modified by descending and local control, allowing the neurons to be reused in different behaviors (Burrows 1996). Anatomical modularity has been suggested to reduce the energy consumption of neural processing by reducing the length of relatively common local connections and increasing the length of relatively rare long-distance connections. Thus, although modularity may be beneficial for efficiency, it may be opposed by neural reuse, which may not minimize the lengths of connections within neural circuits. In small brains, the low number of neurons and the short distances of most connections may promote further functional reuse, even when some components of neural circuits are in different anatomical segments. Thus, in small brains there may be an increased prevalence of neural reuse.